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CULTURAL CHARACTERS AS A GUIDE TO THE TAXONOMY OF THE POLYPORACEAE[1]

Although wood-inhabiting species of Hymenomycetes develop mainly within the host, where their complex physiological activities break down the components of the wood and cause typical brown or white rots, their classification has been based solely on the characters of their fruit bodies, structures which are highly specialized for the protection of basidia and the dispersal of basidiospores. Early systems of classification, in which genera and higher taxonomic units were segregated on the basis of gross morphological characters of fruit bodies and especially the hymenial configuration, are being replaced by systems in which the types of hyphae and their arrangement in fruit bodies are accorded major significance. Corner (1932), in emphasizing the importance in taxonomy of the structure of the tissues of fruit bodies and the nature of the hyphae composing them, recognized three main categories of hyphae, generative hyphae and their modifications to form skeletal and binding hyphae, and three hyphal systems, the monomitic, dimitic, and trimitic. To follow Corner's methods it is necessary to observe the form and arrangement of hyphae composing fruit bodies, a task which becomes very laborious in fruit bodies with complex structure such as those of many species with poroid hymenial surfaces. Fidalgo (1967) recently stressed the difficulty of preparing satisfactory mounts for examination when he resorted to the use of ultrasonic vibrations "to release unbroken hyphae from the plectenchyma and provide better information about the microstructures of the sporophore." Meanwhile, in cultures of all the species, including those whose fruit bodies are so difficult to dissect and whose hyphal systems are difficult to determine, generative hyphae and hyphae modified to form the characteristic microstructures of the species may be observed with ease.

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Pinto-Lopes (1952) recognized this when he reported the occurrence of similar types of hyphae in fruit bodies and cultures of 90 species of Polyporaceae and proposed a classification of the family based on these microstructures. In 1958 I too suggested that certain cultural characters, including the types of generative hyphae and their modifications, could provide a guide to relationships in the Polyporaceae. Ten years later I am still convinced that cultural characters have taxonomic significance and I wish to present the basis for this conviction.

METHODS

I have worked with cultures of wood-inhabiting species of Hymenomycetes for many years, at first for the practical purpose of identifying large numbers of cultures isolated from decays of forest trees in Canada during extensive surveys and more recently in a search for the possible contribution to taxonomy of cultural characters. Cultures of over 600 species of Hymenomycetes have been accumulated, many accompanied by voucher specimens in the Canada Department of Agriculture, Ottawa, Mycological Herbarium, descriptions of over 300 species have been prepared, of which 150 have been published, and the species have been arranged in diagnostic keys to facilitate comparisons between isolates to be identified and named cultures. The standard procedure is to grow cultures for identification or description on agar containing 1.25% Difco Bacto malt extract and 2% Difco Bacto-Agar in Petri dishes from a side inoculum, at room temperature or at 25° C., in the dark, for 6 weeks. At weekly intervals, records are made of the radius of the colony, the rate of growth being expressed as the number of weeks required by the culture to cover the surface of the agar in the Petri dish, the form and character of the advancing zone, the color, topography, and texture of the mat, the presence or absence of fruiting areas, the color changes in the agar induced by the growth of the fungus, and the odor. At suitable intervals, mycelium from the advancing zone, from the older parts of the colony, both aerial and submerged, and from fruiting areas is mounted in aqueous KOH and stained with an aqueous solution of phloxine for the observation and description of hyphal characters.

The presence or absence of extracellular oxidase is determined by the Bavendamm method, in which the cultures are grown for 1 week on malt agar containing 0.5% gallic or tannic acid, when the appearance of brown diffusion zones indicates the formation of extracellular oxidase; the absence of such diffusion zones indicates lack of extracellular oxidase. A rapid method giving comparable results consists of dropping an alcoholic solution of guaiacum on the mat of a growing culture, where the rapid appearance of a blue color indicates the occurrence of extracellular oxidase; no change or a tardy appearance of a pale blue color indicates its absence. The color changes are probably caused by one or more laccases released by the cells into the medium.

DIAGNOSTIC CHARACTERS

Whenever possible, my descriptions of the cultural characters of a species are based on several isolates since these may show some variation in their macroscopic characters, topography, texture, color, and ability to fruit, although they are remarkably uniform in their growth rate at constant temperatures and in their microscopic characters. Since the microstructures produced in culture are constant for each species, major divisions in my diagnostic keys are based on hyphal characters, including the type of septation in generative hyphae and the special structures produced by the differentiation of those hyphae. Four types of generative hyphae occur (Nobles, 1965). In the largest number of species all thin-walled hyphae are nodose-septate. In 17 of the species treated here but in a number of species in other families, thin-walled hyphae in the advancing zone and frequently in the submerged mycelium are simple-septate and these hyphae, usually broad, give off branches which are narrower and nodose-septate, the older part of the mat being composed of such nodose-septate hyphae. In four species treated here but in larger numbers of species of the Coniophoraceae and Stereaceae, the thin-walled hyphae are mainly simple-septate but have occasional single or multiple clamp connections, these occurring most frequently on the hyphae of the advancing zone. In the remaining species, the thin-walled hyphae are simple-septate. Since nearly 80% of the species in this study (exclusive of the 48 species with poroid, xanthochroic fruit bodies more properly assigned to the Hymenochaetaceae) have nodose-septate hyphae throughout or in all regions except the advancing zone and since a number of species in which the septation is usually simple occasionally form clamp connections, it may be postulated that in this group, which represents the family Polyporaceae as it is commonly accepted, the nodose-septate condition was originally universal and that certain species have lost the property of forming clamp connections.

In about 50 of the species treated here the thin-walled generative hyphae remained undifferentiated throughout the period of examination, which extends over 6 weeks in my studies but over only 2 weeks in the studies of some other authors whose data I have used in preparing this paper. There is always the possibility that the apparent absence of differentiated hyphae results from the failure to observe them. However, in many species there is definitely no differentiation of hyphae in culture and it is of interest to observe that the hyphal systems in fruit bodies of many of these species are described as monomitic.

The differentiation of generative hyphae to form fiber hyphae occurs in the cultures of many species. In my terminology, fiber hyphae are hyphae with thick, refractive walls, hyaline or brown, and lumina narrow or apparently lacking, arising as the elongated terminal cell of a hypha and thus aseptate, rarely branched in some species, frequently branched in others. In cultures of many species the fiber hyphae are numerous, long and flexuous, and interwoven to form a thick mat, often coherent and tough. These fiber hyphae are homologous with the skeletal and binding hyphae of fruit bodies and, in general, occur in those species whose fruit body hyphal systems are described as dimitic or trimitic. In a few species fiber hyphae are produced tardily and may not be observed during the 2-week period of observation used by some investigators or even during the 6-week period that I use, but they are readily observed in most species.

In 28 of the species included in the present study, hyphae are differentiated to form nodose-septate hyphae with irregularly thickened walls or with scattered thick-walled, refractive areas on the walls. In some species the walls appear to swell in aqueous KOH while the lumen is reduced to a narrow line with occasional expansions, often running from side to side of the hypha. The clamp connections may become enlarged, thick-walled, and in appearance suggest a ball-and-socket bone structure. In other species, the first indication of this type of differentiation is the formation of hyphae with numerous short branches or protuberances whose walls are thick or solid and refractive. These thick-walled nodose-septate hyphae occur unaccompanied by fiber hyphae in cultures of *Leptotrimitus semipileatus* (Peck) Pouz., *Poria placenta* (Fr.) Cke, and others and in association with numerous fiber hyphae in *Daedalea* spp., *Fomes cajanderi* Karst., etc. They were recorded in fruit bodies of *Coriolellus* (*Daedalea*) spp. by Sarkar (1959) and in those of *Osteina obducta* (Berk.) Donk by Donk (1966b), and were included in the diagnostic characters of the genus *Daedalea* by Aoshima (1967).

In a number of species, generative hyphae differentiate to form cuticular cells, which originate as terminal or intercalary swellings, at first hyaline with contents staining in phloxine, finally with walls slightly thickened and remaining hyaline or becoming brown. These are crowded to form pseudo-parenchymatous areas which appear skinlike or crustose on the surface of mycelial mats or form translucent sheets in the submerged mycelium. Cuticular cells accompanied by fiber hyphae are characteristic of cultures of *Ganoderma* spp. and may be homologous with the inflated hyphal ends that form the upper crust of fruit bodies of species in that genus. In poroid species of the Hymenochaetaceae with xanthochroic fruit bodies, cuticular cells interwoven with fiber hyphae occur in *Fomes igniarius* (L. ex Fr.) Kickx and its varieties and in some isolates of *Poria obliqua* (Pers. ex Fr.) Karst. Cuticular cells without accompanying fiber hyphae form coherent surface layers or sheets in the agar in cultures of *Heterobasidion annosum* (Fr.) Bref. and *Rigidoporus* spp.

In a number of other species dark-colored skinlike surface layers are composed of hyphae with numerous short, hooked, or recurved branches, as in *Polyporus vulpinus* Fr., *Poria tsugina* (Murr.) Sacc. & Trott., and *Polyporus radiatus* Sow. ex Fr. of the Hymenochaetaceae or of hyphae with irregular, thick-walled branches, nodules, or protuberances as in cultures of species of *Polyporus s. st.*

Hyphae with contorted tips, heavily incrusted, are conspicuous in mounts of aerial mycelium from cultures of *Climacocystis borealis* (Fr.) Kotl. & Pouz., *Leptotrimitus semipileatus* (Peck) Pouz., and *Incrustoporia* spp. They appear to be specialized structures, differing from the lightly incrusted hyphae or hyphal segments that occur in cultures of many species. Similar incrusted hyphal tips in the ends of dissepiments of fruit bodies of *Poria* (*Incrustoporia*) *stellae* Pil. and *P. tschulymica* Pil. were described by Eriksson (1958).

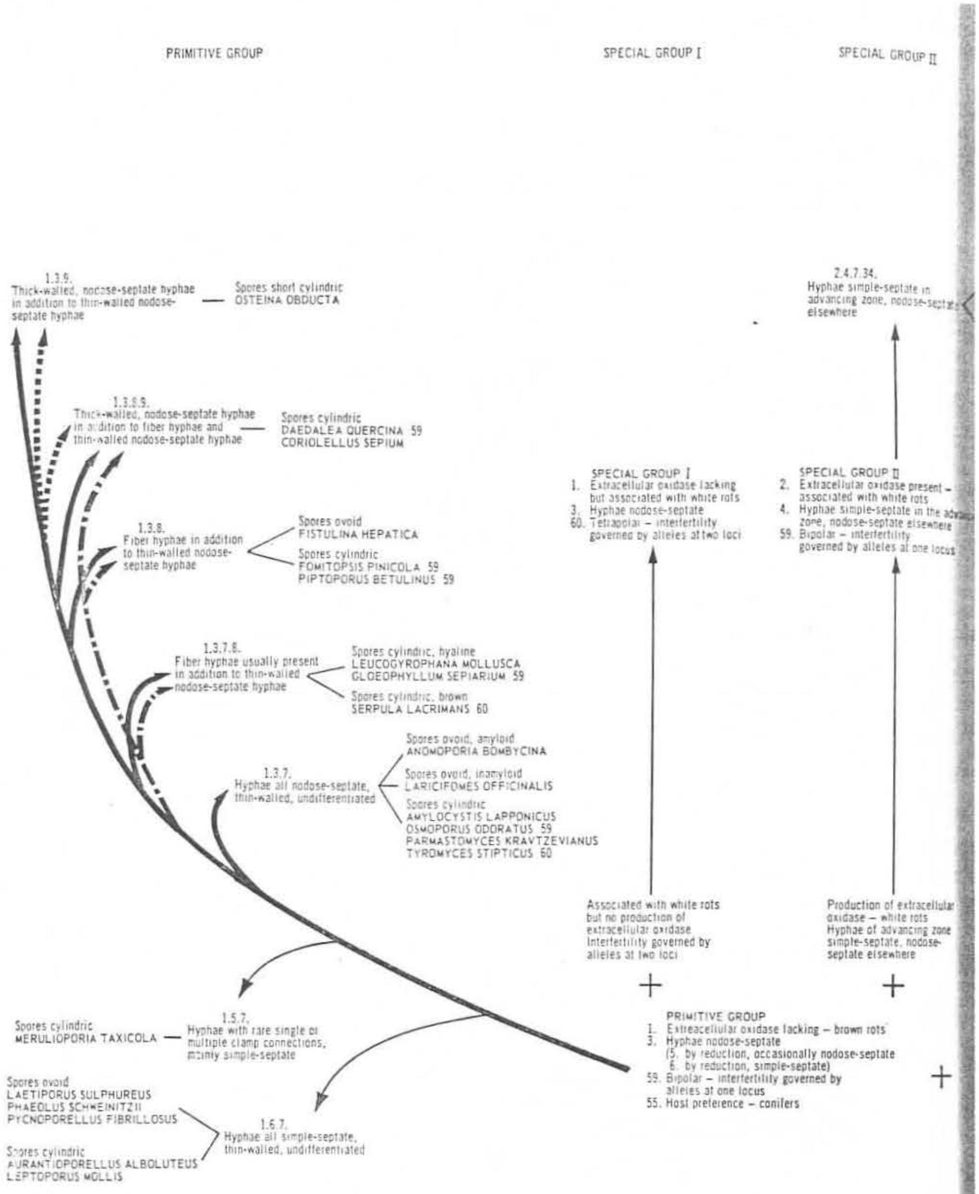
Other microstructures formed by the differentiation of hyphae in cultures include cystidia and gloeocystidia, setae and setal hyphae, swellings of various types, and conidia, chlamydospores, and oidia. Such structures are included in descriptions of cultures of individual species and are useful in diagnosis but they appear to have little or no taxonomic significance above the species level and so are not discussed here. Similarly, growth rates and the appearançe of cultures may provide clues for the identification of individual cultures but they play no part in segregating groups of related species and so are omitted from the discussion.

Earlier I remarked that the vegetative phase in the life cycle of wood-rotting fungi has not been considered in taxonomy although the results of its enzymatic activity can be readily observed. Decays in wood caused by these fungi are divided into two main types, the brown rots, in which the cellulose content is reduced while the lignin component remains practically constant, and the white rots in which both cellulose and lignin are attacked. It seems reasonable to assume that the species that cause both brown and white rots possess an enzyme system capable of reducing cellulose and that those species associated with white rots have acquired a second enzyme system involved in the degradation of lignin. The question is whether the enzyme system involved in lignin breakdown was acquired independently by each of the species associated with white rots or whether, in the course of evolution, this enzyme system was developed on one or only a few occasions. If lignin-degrading enzyme systems were developed independently by the species causing white rots, then such species do not necessarily demonstrate kinship by their possession of these enzymes and may be related to different parent species that cause brown rots. I believe that the evidence supports the alternate hypothesis, that the enzyme systems involved in lignin breakdown developed on one or only a few occasions and that the species in which these enzymes occur are more closely related among themselves than with the species that cause no appreciable lignin degradation.

When the Bavendamm or alcoholic gum guaiacum test for extracellular oxidase is applied to cultures of wood-rotting Hymenomycetes, with few exceptions cultures of species that cause brown rots show no color change, whereas those that cause white rots show the color changes that indicate the presence of extracellular oxidase. There is no claim that this enzyme, probably a laccase, is responsible for lignin degradation but its occurrence is apparently linked with that of the enzyme system that is involved.

Information on interfertility phenomena is available for 85 of the 275 species included in the present study, three species being homothallic and 82 species being heterothallic; 27 showing the bipolar type of interfertility governed by alleles at one locus, 52 the tetrapolar type of interfertility governed by alleles at two loci, with 3 heterothallic species for which the type of interfertility was not determined. Of species whose cultures do not produce extracellular oxidase, 3 are homothallic, 2 are heterothallic but the type is not known, 16 are bipolar, and 4 are tetrapolar. Of the species whose cultures produce extracellular oxidase and whose generative hyphae are regularly nodose-septate, 48 are tetrapolar, 2 are bipolar, whereas 9 species with generative hyphae simple-septate in the advancing zone and nodose-septate elsewhere are bipolar. This suggests strongly that, in general, bipolarity is the usual type of interfertility in species that lack extracellular oxidase and are associated with brown rots and that tetrapolarity is the usual type of interfertility in species associated with white rots, whose cultures produce extracellular oxidase and are regularly nodose-septate.

The classification of the Polyporaceae based on cultural characters that I am now presenting is essentially the same as the one that I published in 1958 and presented in a demonstration paper at the Ninth International Botanical Congress in 1959. In that scheme, the groups of species brought together in the final divisions were listed alphabetically according to genus and species, the generic names being those used by Overholts, Lowe, and other conservative taxonomists. I am now attempting to correlate the information on relationships within the Polyporaceae provided by cultural studies with recent systems of classification. The suggested classification is shown diagrammatically in figure 1 in which only species that have been designated as types of genera are listed and in table 2 where the species that compose each of the final groups are listed, with the type species preceded by an asterisk. Following a system of notation used in my key for the identification of cultures of wood-inhabiting


PRIMITIVE GROUP
SPECIAL GROUP I
SPECIAL GROUP II
1.3.9.
Thick-walled, nodose-septate hyphae in addition to thin-walled nodose-septate hyphae
Spores short cylindric
OSTEINA OBDUCTA
1.3.8.9.
Thick-walled, nodose-septate hyphae in addition to fiber hyphae and thin-walled nodose-septate hyphae
Spores cylindric
DAEDALEA QUERCINA 59
CORIOLELLUS SEPIUM
1.3.8.
Fiber hyphae in addition to thin-walled nodose-septate hyphae
Spores ovoid
FISTULINA HEPATICA
Spores cylindric
FOMITOPSIS PINICOLA 59
PIPTOPORUS BETULINUS 59
1.3.7.8.
Fiber hyphae usually present in addition to thin-walled nodose-septate hyphae
Spores cylindric, hyaline
LEUCOGYROPHANA MOLLUSCA
GLOEOPHYLLUM SEPIARIUM 59
Spores cylindric, brown
SERPULA LACRIMANS 60
1.3.7.
Hyphae all nodose-septate, thin-walled, undifferentiated
Spores ovoid, amyloid
ANOMOPORIA BOMBYCINA
Spores ovoid, inamyloid
LARICIFOMES OFFICINALIS
Spores cylindric
AMYLOCYSTIS LAPPONICUS
OSMOPORUS ODORATUS 59
PARMASTOMYCES KRAVTZEVIANUS
TYROMYCES STIPTICUS 60
1.5.7.
Hyphae with rare single or multiple clamp connections, mainly simple-septate
Spores cylindric
MERULIOPORIA TAXICOLA
1.6.7.
Hyphae all simple-septate, thin-walled, undifferentiated
Spores ovoid
LAETIPORUS SULPHUREUS
PHAEOLUS SCHWEINITZII
PYCNOPORELLUS FIBRILLOSUS
Spores cylindric
AURANTIOPORELLUS ALBOLUTEUS
LEPTOPORUS MOLLIS
SPECIAL GROUP I
1. Extracellular oxidase lacking but associated with white rots
3. Hyphae nodose-septate
60. Tetrapolar – interfertility governed by alleles at two loci
Associated with white rots but no production of extracellular oxidase Interfertility governed by alleles at two loci
+
2.4.7.34.
Hyphae simple-septate in advancing zone, nodose-septat
elsewhere
SPECIAL GROUP II
2. Extracellular oxidase present – associated with white rots
4. Hyphae simple-septate in the adv
zone, nodose-septate elsewhere
59. Bipolar – interfertility governed by alleles at one locus
Production of extracellular oxidase – white rots Hyphae of advancing zone simple-septate, nodose-septate elsewhere
+
PRIMITIVE GROUP
1. Extreacellular oxidase lacking – brown rots
3. Hyphae nodose-septate
(5. by reduction, occasionally nodose-septate
6. by reduction, simple-septate)
59. Bipolar – interfertility governed by alleles at one locus
55. Host preference – conifers
+

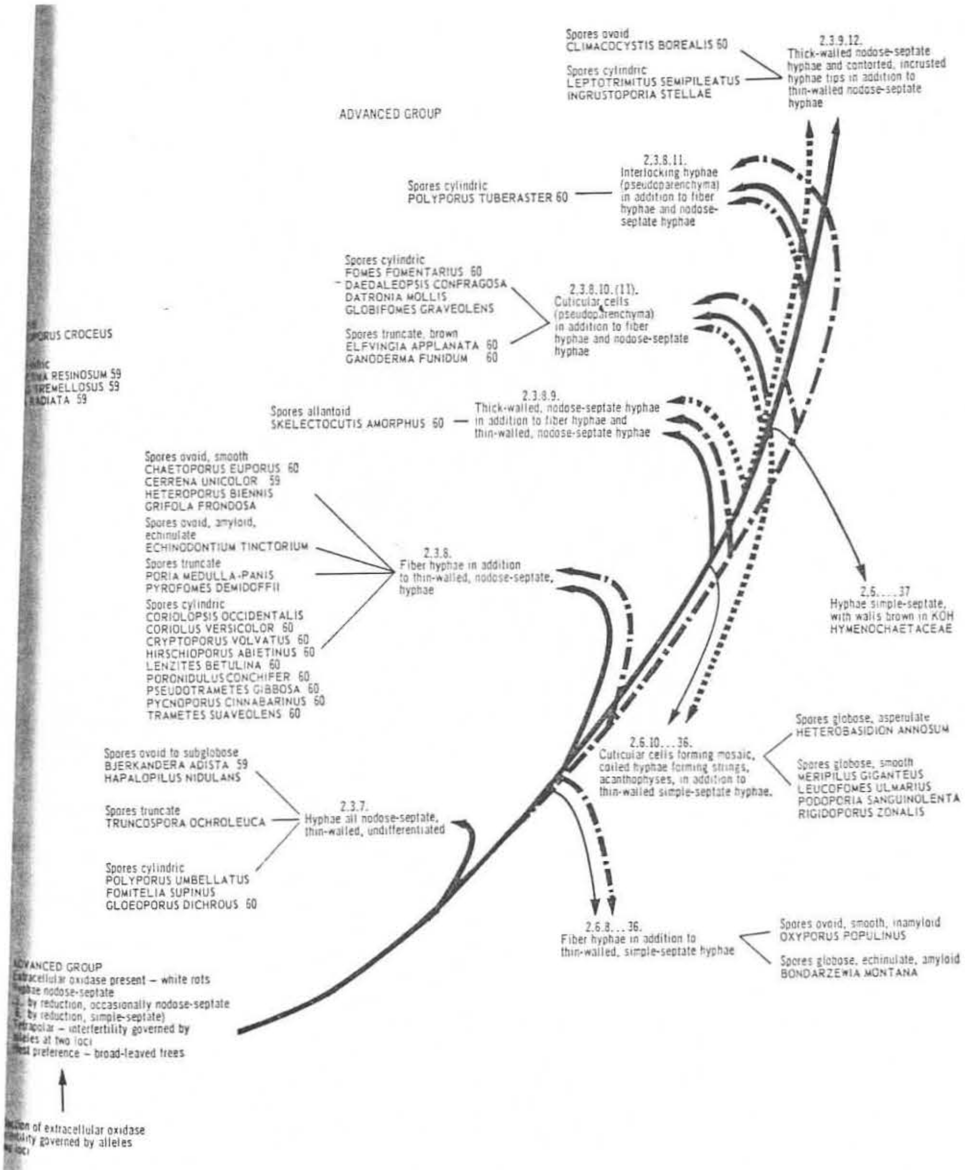

Spores ovoid
CLIMACOCYSTIS BOREALIS 60
Spores cylindric
LEPTOTRIMITUS SEMIPILEATUS
INGRUSTOPORIA STELLAE
2.3.9.12.
Thick-walled nodose-septate hyphae and contorted, incrusted hyphae tips in addition to thin-walled nodose-septate hyphae
ADVANCED GROUP
Spores cylindric
POLYPORUS TUBERASTER 60
2.3.8.11.
Interlocking hyphae (pseudoparenchyma) in addition to fiber hyphae and nodose-septate hyphae
Spores cylindric
FOMES FOMENTARIUS 60
DAEDALEOPSIS CONFRAGOSA
DATRONIA MOLLIS
GLOBIFOMES GRAVEOLENS
Spores truncate, brown
ELFVINGIA APPLANATA 60
GANODERMA FUNIDUM 60
2.3.8.10.(11).
Cuticular cells (pseudoparenchyma) in addition to fiber hyphae and nodose-septate hyphae
RUS CROCEUS
A RESINOSUM 59
TREMELLOSUS 59
ADIATA 59
Spores allantoid
SKELECTOCUTIS AMORPHUS 60
2.3.8.9.
Thick-walled, nodose-septate hyphae in addition to fiber hyphae and thin-walled, nodose-septate hyphae
Spores ovoid, smooth
CHAETOPORUS EUPORUS 60
CERRENA UNICOLOR 59
HETEROPORUS BIENNIS
GRIFOLA FRONDOSA
Spores ovoid, amyloid, echinulate
ECHINODONTIUM TINCTORIUM
Spores truncate
PORIA MEDULLA-PANIS
PYROFOMES DEMIDOFFII
Spores cylindric
CORIOLOPSIS OCCIDENTALIS
CORIOLUS VERSICOLOR 60
CRYPTOPORUS VOLVATUS 60
HIRSCHIOPORUS ABIETINUS 60
LENZITES BETULINA 60
PORONIDULUS CONCHIFER 60
PSEUDOTRAMETES GIBBOSA 60
PYCNOPORUS CINNABARINUS 60
TRAMETES SUAVEOLENS 60
2.3.8.
Fiber hyphae in addition to thin-walled, nodose-septate, hyphae
2.6.....37
Hyphae simple-septate, with walls brown in KOH
HYMENOCHAETACEAE
Spores globose, asperulate
HETEROBASIDION ANNOSUM
2.6.10...36.
Cuticular cells forming mosaic, coiled hyphae forming strings, acanthophyses, in addition to thin-walled simple-septate hyphae.
Spores globose, smooth
MERIPILUS GIGANTEUS
LEUCOFOMES ULMARIUS
PODOPORIA SANGUINOLENTA
RIGIDOPORUS ZONALIS
Spores ovoid to subglobose
BJERKANDERA ADISTA 59
HAPALOPILUS NIDULANS
Spores truncate
TRUNCOSPORA OCHROLEUCA
2.3.7.
Hyphae all nodose-septate, thin-walled, undifferentiated
Spores cylindric
POLYPORUS UMBELLATUS
FOMITELIA SUPINUS
GLOEOPORUS DICHROUS 60
2.6.8...36.
Fiber hyphae in addition to thin-walled, simple-septate hyphae
Spores ovoid, smooth, inamyloid
OXYPORUS POPULINUS
Spores globose, echinulate, amyloid
BONDARZEWIA MONTANA
ANCED GROUP
acellular oxidase present – white rots
e nodose-septate
by reduction, occasionally nodose-septate
by reduction, simple-septate)
polar – interfertility governed by
les at two loci
preference – broad-leaved trees
n of extracellular oxidase
ity governed by alleles

FIGURE 1. Cultural characters as a guide to the taxonomy of the Polyporaceae.

TABLE 1. DIAGNOSTIC CHARACTERS AND THEIR CODE SYMBOLS.

Code Symbol 1.	Results negative in tests for extracellular oxidase
Code Symbol 2.	Results positive in tests for extracellular oxidase
Code Symbol 3.	Thin-walled hyphae consistently nodose-septate
Code Symbol 4.	Thin-walled hyphae simple-septate in the advancing zone, nodose-septate elsewhere
Code Symbol 5.	Thin-walled hyphae mainly simple-septate, with occasional single or multiple clamp connections
Code Symbol 6.	Thin-walled hyphae consistently simple-septate
Code Symbol 7.	Hyphae remaining thin-walled and undifferentiated
Code Symbol 8.	Hyphae differentiated to form fiber hyphae
Code Symbol 9.	Hyphae differentiated to form nodose-septate hyphae with irregularly thickened walls or with scattered thick refractive areas on walls
Code Symbol 10.	Hyphae differentiated to form cuticular cells, closely packed to form a pseudo-parenchyma
Code Symbol 11.	Hyphae differentiated through formation of numerous short branches, hooked or recurved, or thick-walled nodules, interlocked to form a plectenchyma.
Code Symbol 12.	Hyphae differentiated to form numerous contorted incrusted hyphal tips
Code Symbol 36.	Hyphae hyaline and mats white or pale in color
Code Symbol 37.	Hyphae yellow or brown when mounted in KOH solution and mats yellow or brown, at least in part
Code Symbol 57.	Species homothallic, completing the life cycle from a single basidiospore
Code Symbol 58.	Heterothallic, but type of interfertility not known
Code Symbol 59.	Heterothallic, showing the bipolar type of interfertility
Code Symbol 60.	Heterothallic, showing the tetrapolar type of interfertility

TABLE 2. A CLASSIFICATION OF THE "POLYPORACEAE" BASED ON CULTURAL CHARACTERS.

Key Code 1.3.7.

Spores ovoid, amyloid

Anomoporia albolutescens
°*Anomoporia bombycina*

Spores, ovoid, inamyloid

°*Laricifomes officinalis*
°*Leucogyrophana molluscus*
"Polyporus" anthracophilus
"Polyporus" australiensis
"Polyporus" balsameus
"Polyporus" guttulatus
"Polyporus" portentosus
"Poria" aneirina
"Poria" crassa

Spores cylindric, hyaline

°*Amylocystis lapponicus*
°*Osmoporus odoratus*—59

Spores cylindric, hyaline—continued

°*Parmastomyces kravtzevianus*
"Poria" carbonica
"Poria" gossypium
"Poria" radiculosa
"Poria" sequoiae

Spores cylindric, brown

°*Meruliporia incrassata*
"Merulius" aureus
"Merulius" lignicola
Serpula pinastri

Spores allantoid, small, hyaline

"Merulius" niveus
"Polyporus" caesius
"Polyporus" fragilis
"Poria" pannocincta

Key Code 1.3.8.36.

Spores ovoid

°*Fistulina hepatica*
"Polyporus" spraguei
"Poria" vaillantii
"Polyporus" meliae—59
"Polyporus" palustris—59
"Polyporus" rubidus
"Trametes" dickinsii

Spores cylindric

°*Fomitopsis pinicola*—59
Fomitopsis rosea—59

Spores allantoid, small

°*Piptoporus betulinus*—59

Key Code 1.3.8.37.

Spores ellipsoid, brown

"Poria" nigra
Serpula himantioides—60
°*Serpula lacrimans*—60

Spores cylindric, hyaline

Gloeophyllum abietinum—59
°*Gloeophyllum sepiarium*—59
°*Phaeocoriolellus trabeus*—59
"Lenzites" striata
"Trametes" carbonaria

TABLE 2. A CLASSIFICATION OF THE "POLYPORACEAE" (*Cont'd*).

Key Code 1.3.8.9.

Spores cylindric

- *Coriolellus heteromorphus*—59
- *Coriolellus malicola*—57
- °*Coriolellus sepium*—58
- *Coriolellus serialis*—59
- *Coriolellus sinuosus*—58
- *Coriolellus variiformis*—59
- °*Daedalea quercina*—59

Spores cylindric—continued

- *"Fomes" cajanderi*—59
- *"Polyporus" durus*
- *"Trametes" lilacino-gilva*

Spores allantoid, small

- *"Poria" alpina*
- *"Poria" xantha*

Key Code 1.3.9.

Spores oblong or short cylindric

- °*Osteina obducta*
- *"Poria" oleracea*
- *"Poria" placenta*—59
- *"Poria" sericeomollis*

Spores allantoid, small

- *Tyromyces albo-brunneus*
- °*Tyromyces stipticus*—60
- *Tyromyces tephroleucus*—59
- *Tyromyces undosus*

Key Code 1.5. (multiple) 7.

Spores short cylindric or allantoid

- *"Merulius" ambiguus*
- *"Merulius" corium*—57
- *"Poria" griseoalba*
- *"Poria" taxicola*—57

Key Code 1.2.6.7.

- °*Aurantioporellus alboluteus*
- °*Laetiporus sulphureus*
- °*Leptoporus mollis*
- *"Merulius" confluens*
- °*Phaeolus schweinitzii*
- °*Pycnoporellus fibrillosus*
- *"Poria" aurea*
- *"Poria" cocos*
- *"Poria" inflata*
- *"Poria" metamorphosa*
- *"Poria" reticulata*
- *"Poria" rhodella*
- *"Poria" spissa*

Key Code 2.3.7.

Spores globose, echinulate

- *"Poria" candidissima*

Spores ovoid, smooth—continued

- *"Polyporus" fumidiceps*

TABLE 2. A CLASSIFICATION OF THE "POLYPORACEAE" (*Cont'd*).

Spores truncate

- °*Truncospora ochroleuca*
- *Truncospora ohiensis*

Spores ovoid, smooth

- °*Bjerkandera adusta*–59
- *Bjerkandera fumosa*–60
- °*Hapalopilus nidulans*
- *"Polyporus" consors*
- *"Polyporus" delectans*–60
- *"Polyporus" fissilis*
- *"Polyporus" peckianus*
- *"Poria" overholtsii*
- *"Poria" versipora*

Spores cylindric

- °*Fomitella supina*–60
- *"Polyporus" hirtus*
- *"Polyporus" umbellatus*
- *"Poria" mappa*

Spores allantoid

- °*Gloeoporus dichrous*–60
- *"Poria" crustulina*

Key Code 2.3.8.

Spores subglobose to ellipsoid, chlamydospores very numerous

- °*Grifola frondosa*
- °*Heteroporus biennis*
- *"Polyporus" obtusus*–60
- *"Polyporus" robiniophilus*
- *"Polyporus" spumeus* var. *mongolica*
- *"Trametes" cingulata*
- *"Trametes" ljubarskyi*–60

Spores ellipsoid, amyloid, echinulate

- °*Echinodontium tinctorium*

Spores truncate, hyaline

- *"Fomes" ellisianus*–60
- *"Fomes" fraxinophilus*–60
- *"Polyporus" compactus*–60
- °*Poria medulla-panis*
- *Poria subacida*
- *Poria tenuis* var. *pulchella*

Spores cylindric

- °*Chaetoporus euporus*–60
- *Chaetoporus rixosa*
- *Chaetoporus variecolor*
- °*Coriolopsis occidentalis*
- *Coriolus hirsutus*–60
- *Coriolus pinsitus*
- *Coriolus pubescens*–60
- °*Coriolus versicolor*–60
- *Coriolus zonatus*–60
- °*Cryptoporus volvatus*–60
- *"Daedalea" ambigua*
- °*Dichomitus squalens*–60
- *Favolus alveolaris*–60
- °*Globifomes graveolens*
- °*Hirschioporus abietinus*–60
- *Hirschioporus fusco-violaceus* –60
- *Hirschioporus laricinus*–60
- *Hirschioporus pergamenus*–60
- °*Lenzites betulina*–60
- *Lenzites flaccida*
- *Lenzites palisoti*
- *Lenzites reichardtii*–60
- *"Polystictus" leoninus*
- *"Polystictus" xanthopus*–60

TABLE 2. A CLASSIFICATION OF THE "POLYPORACEAE" (*Cont'd*).

Spores oblong—ellipsoid

°*Cerrena unicolor*—59
"*Poria*" *aestivale*
"*Poria*" *albidofusca*—60
"*Poria*" *fissiliformis*

Spores truncate, brown

°*Phaeotrametes decipiens*—58
"*Polyporus*" *megaloporus*—60
°*Pyrofomes demidoffii*

°*Poronidulus conchifer*—60
°*Pseudotrametes gibbosa*—60
°*Pycnoporus cinnabarinus*—60
Pycnoporus coccineus—60
Pycnoporus sanguineus—60
Trametes flavescens—60
Trametes hispida—60
Trametes meyenii
Trametes proteus
°*Trametes suaveolens*—60
Trametes trogii—60

Key Code 2.3.8.9.

Spores allantoid

°*Skeletocutis amorphus*—60

Key Code 2.3.8.10.

Spores subglobose, hyaline, smooth

"*Fomes*" *fraxineus*—60

Spores truncate, brown, appearing echinulate

Amauroderma rude

Spores truncate, etc.—continued

°*Elfvingia applanata*—60
Ganoderma colossum
Ganoderma lobatum
°*Ganoderma lucidum*—60
Ganoderma oregonense
Ganoderma tsugae
Ganoderma resinaceum

Key Code 2.3.8.10.11.

Spores cylindric

°*Daedaleopsis confragosa*
Daedaleopsis confragosa
var. *Lenzites tricolor*
°*Datronia mollis*—60
°*Fomes fomentarius*—60
Fomes sclerodermeus
Fomes scutellatus
"*Lenzites*" *eximia*
"*Trametes*" *campestris*—60

TABLE 2. A CLASSIFICATION OF THE "POLYPORACEAE" (*Cont'd*).

Key Code 2.3.8.11.

Spores cylindric

- *Polyporus arcularius*—60
- *Polyporus brumalis*—60
- *Polyporus elegans*
- *Polyporus melanopus*
- *Polyporus platensis*

Spores cylindric—continued

- *Polyporus radicatus*
- *Polyporus squamosus*—60
- *Polyporus tuberaster*—60
- *Polyporus varius*

Key Code 2.3.9.12.

Spores ovoid

- °*Climacocystis borealis*—60

Spores allantoid

- °*Incrustoporia stellae*
- *Incrustoporia subincarnata*

Spores allantoid—continued

- *Incrustoporia tschulymica*
- °*Leptotrimitus semipileatus*
- "*Polyporus*" *albellus*—60
- "*Poria*" *odora*

Key Code 2.4.7.

Spores ovoid

- °*Aurantioporus croceus*
- *Merulius porinoides*—59
- *Phlebia atkinsoniana*
- "*Polyporus*" *galactinus*—59
- "*Polyporus*" *pulcherrimus*
- "*Poria*" *mutans*
- "*Poria*" *rivulosa*—59
- "*Poria*" *salmonicolor*
- "*Radulum casearium*"—59

Spores allantoid

- *Ischnoderma benzoinum*
- °*Ischnoderma resinosum*—59
- °*Merulius tremellosus*—59
- *Phlebia albida*
- °*Phlebia radiata*—59
- "*Poria*" *cinerascens*—59
- "*Poria*" *subvermispora*—59
- "*Poria*" *zonata*

Key Code 2.6.8.

Spores ovoid, smooth, inamyloid

- °*Oxyporus populinus*

Spores cylindric

- °*Irpex lacteus*

Spores globose, echinulate, amyloid

- *Bondarzewia berkeleyi*
- °*Bondarzewia montana*

TABLE 2. A CLASSIFICATION OF THE "POLYPORACEAE" (*Cont'd*).

Key Code 2.6.10.

Spores globose, asperulate

- °*Heterobasidion annosum*

Spores globose, smooth

- °*Meripilus giganteus*
- *"Polyporus" catevatus*
- *"Polyporus" rigidus*
- *"Polyporus" rugulosus*
- *"Poria" adiposa*

Spores globose, smooth—continued

- *"Poria" hypolateritia*
- *"Poria" vincta*
- *Rigidoporus latemarginatus*
- *Rigidoporus lignosus*
- *Rigidoporus nigrescens*
- *Rigidoporus sanguinolentus*
- *Rigidoporus ulmarius*
- *Rigidoporus vitreus*
- *Rigidoporus zonalis*

Key Code 2.3.37.

Hymenochaetaceae 48 species

Hymenomycetes (Nobles, 1965), subdivisions are headed by key codes, a series of numbers (referred to as Code Symbols), each of which denotes a cultural character. The Code Symbols for those cultural characters which I have discussed above and to which I attribute taxonomic significance above the species level are listed in table 1.

A Species Code, the series of Code Symbols that denote the cultural characters shown by cultures of a species, was prepared for each of the 275 species in the study from descriptions made in my laboratory or published by a number of authors. With the exception of 12 species belonging to *Merulius, Phlebia, Echinodontium,* and *Radulum,* all the species have fruit bodies with poroid hymenial configuration, the mark of the family Polyporaceae as it is commonly accepted. By sorting the Species Codes an arrangement of species that may indicate relationships was obtained.

As shown in figure 1, the first division is based on the results of tests for extracellular oxidase, the species whose cultures produced no extracellular oxidase being shown on the left side of the chart under Code Symbol 1, those whose cultures produced extracellular oxidase being on the right side under Code Symbol 2. The cultures of 70 species gave consistently negative results, 183 gave consistently positive results, and 22 species gave negative results in some tests, positive in others. On the basis of the types of their associated rots, 13 of the 22 species were assigned to the group whose cultures lack extracellular oxidase, 9 to the group whose cultures produce oxidase. In the chart, the heavy solid line indicates that the generative hyphae are nodose-septate so that all the species above these lines in groups designated by Key Codes 1.3. and 2.3. have generative hyphae that are regularly nodose-septate whereas species in the group designated by Key Code 2.4. have generative hyphae that are simple-septate in the advancing zone, nodose-septate elsewhere. The groups below the heavy solid line, with Key Codes 1.5., 1.6., 2.6., consist of species whose generative hyphae are simple-septate or have rare single or multiple clamp connections, which I interpret as a form of reduction. The species in whose cultures the generative hyphae remain undifferentiated or at least show none of the modifications considered to have taxonomic value above the species level fall under Key Codes 1.3.7. and 2.3.7. Above these, the dash-dot lines indicate the differentiation of nodose-septate hyphae to form fiber hyphae, which appear tardily or may be lacking in species under Key Code 1.3.7.8., but are present in all species under 1.3.8. and 2.3.8. The dotted lines indicate the differentiation of generative hyphae to form thick-walled nodose-septate hyphae, present in association with fiber hyphae in groups under Key Codes 1.3.8.9. and 2.3.8.9. and alone in groups designated by Key Codes 1.3.9. and 2.3.9. In the left-hand group, this is the highest degree of differentiation observed. On the right side, cuticular cells, indicated by a dotted line and the Code Symbol 10, and interlocking hyphae, indicated by dash-dot-dot and Code Symbol 11, represent the highest degree of differentiation observed.

The decision to introduce basidiospore morphology as the basis for the final divisions in a classification based on cultural characters resulted from two observations. In well-defined genera composed of species whose fruit bodies and cultures show clear evidence of relationship, such as *Polyporus s. st.*, *Daedalea*, and *Hirschioporus*, basidiospore form and even size are uniform. Hence, genera whose component species show a wide range in basidiospore characters may be suspect. Also, when preparing my paper on classification of the Polyporaceae in 1958, I compared the cultures (in tubes) for the species in each group and even by this crude method was able to recognize similarity among species in some groups while other groups were heterogeneous in respect to characters other than oxidase production and hyphal differentiation. When cultures of species in these heterogeneous groups were sorted into groups of species with similar basidiospore characters, groups of species more uniform in appearance were obtained. Hence, the decision to include a noncultural character was made.

With few exceptions, all the species that fall under Key Code 1.3. on the left side of the chart above the solid line are alike in lacking extracellular oxidase, in being associated with brown rots, in having the bipolar type of interfertility governed by alleles at one locus, and in showing a host preference for conifers. The 17 species with rare clamps or simple septa also lack oxidase, are associated with brown rots, and in at least two species are homothallic. I interpret lack of oxidase, association with brown rots, bipolarity, and a host preference for conifers as primitive characters and therefore describe the group as a primitive one. As noted earlier, differentiation of hyphae in this group results in formation of only fiber hyphae and nodose-septate hyphae with thick walls.

In contrast, all the species that fall under Key Code 2.3. on the right side of the chart above the solid line are alike in producing extracellular oxidase, in causing the breakdown of lignin and the formation of white rots in wood, in having the tetrapolar type of interfertility governed by alleles at two loci, and in showing a host preference for broad-leaved trees. In addition, their hyphae show a high degree of differentiation, with formation of pseudo-parenchymatous areas in cultures, formed of microstructures which may be homologous with microstructures in fruit bodies that characterize the stipitate species of *Polyporus s. st.* and the hard upper surfaces of *Ganoderma* spp. Even in species reduced in the sense that their hyphae lack clamp connections, fiber hyphae occur in *Oxyporus populinus* and cuticular cells and other highly specialized structures in *Rigidoporus* spp. It is of interest also that ovoid to cylindric spores occur in both major divisions but that truncate spores occur only in species on the right side of the chart, where species with truncate spores occur under Key Code 2.3.7. in *Truncospora* spp., under Key Code 2.3.8. in *Poria* spp. and *Pyrofomes demidoffii,* and under Key Code 2.3.8.10. in *Elfvingia applanata* and *Ganoderma* spp., which may suggest a sequence in development within the main group. The number of advanced characters (extracellular oxidase production, ability to degrade lignin and cause white rots, tetrapolarity, host preference for broad-leaved trees, and highly differentiated hyphal structures) common to all species on the right of the chart under Key Codes 2.3. and 2.6.36. (excluding Hymenochaetaceae) suggests that these are related species and represent a monophyletic line of development.

Special Group II, denoted by Key Code 2.4.7.34., is composed of 17 species which may be considered advanced in their production of extracellular oxidase and association with white rots, primitive in their bipolar type of interfertility, and reduced in that hyphae of the advancing zone and submerged mycelium lack clamp connections. In discussing this group in 1958, I wrote

> The cultures show other remarkable similarities: in all, the rate of growth is rapid, the surface of the agar in Petri dishes being covered in one to two weeks; in all but *Polyporus resinosus* and *Radulum casearium*, many of the broad, simple-septate hyphae become thick-walled, the walls appearing to be gelatinously modified; characteristic globose chlamydospores are present and usually numerous in all species except *Merulius rufus* and *Phlebia merismoides*; in these two species and in *Poria rubens*, oidia are produced in abundance, and they occur sparingly in *P. albipellucida* and *P. cinerascens*; and finally, the eight species in the group whose type of interfertility is known are bipolar, in contrast to other species that give a positive test for extracellular oxidase and are tetrapolar. The number and nature of the correlated characters common to all the species suggest that the group is of monophyletic origin. The independent development of the same complex of diverse characters in unrelated species, with the formation of such a group through convergent evolution, seems unlikely.

Boidin (1958) recognized the same group of correlated characters in cultures of certain species of *Merulius*, *Phlebia*, and *Corticium* Sect. *Ceracea*, and in addition similarities in the distribution of nuclei in germinating spores, monocaryotic and dicaryotic mycelia. He too suggested close relationship or convergent evolution as possible explanations of the similarities. Along with the *Corticium* spp. that Boidin included, the *Phlebia* spp. and *Merulius* spp. that we both included, and the species with poroid hymenial configuration in my list, at least one member of the Agaricaceae, *Panellus serotinus* (Pers.) Kühner, has similar cultural characters. To me the group represents a single line of evolution, in which the various types of hymenial configuration and growth habit have developed independently.

In a survey such as this it is possible to observe general lines of development that may reflect phylogeny but quite impossible to look at each of the 32 groups into which the species have been sorted and assess the significance of these groups in taxonomy. In general, species in genera clearly defined by the characters of their fruit bodies show equally striking similarities in their cultures. For example, in table 2 under Key Code 2.3.8.11. nine species of *Polyporus s. st.*, including its type, are listed. The cultures are alike in hyphal characters and in macroscopic appearance, the dark brown, wrinkled, pseudo-parenchymatous areas contrasting sharply with the white cottony or woolly mats. The fruit bodies are alike in being stipitate with at least the basal portion of the stipe covered with a dark-colored cuticle similar to that produced in culture. The basidiospores are large, cylindric, or ellipsoid-cylindric. *Polyporus umbellatus*, which Pouzar (1966) designated as type of *Polyporus* subg. *Dendropolyporus*, and *P. hirtus* lack the fiber hyphae and interlocking hyphae which occur in cultures of *Polyporus spp.* and should, on the evidence from cultural studies, be excluded from *Polyporus s. st.*

Under Key Code 2.3.8.10. (spores truncate, brown, appearing echinulate), one species of *Amauroderma*, one of *Elfvingia*, and six of *Ganoderma* all appear similar in cultural characters, which indicates that they are closely related if not congeneric. Under this Key Code and under Key Code 2.3.8.10.11., which is an admission that the plectenchyma formed in the cultures was so compact that I could not determine whether it was composed of cuticular cells or interlocking hyphae, are eight species with cylindric spores, including the types of *Daedaleopsis*, *Datronia*, and *Fomes*, and one species, *Fomes fraxineus*, with subglobose spores. The similarities in cultural characters suggest relationship and indicate the need for correlated studies of cultures and fruit bodies of the species in the group. The cultural characters of one species, *Trametes campestris*, were described recently by David (1967) and by Domanski and Orlicz (1966). In both papers, the Species Code following my system of notation was given. Code Symbol 11, indicating the presence of interlocking hyphae forming a plectenchyma appeared in both and Domanski and Orlicz described an extensive "layer of plectenchymatous structure" on the surface of cultures. These authors compared this Species Code with that of *T. squalens*, the type of *Dichomitus* Reid, which lacks Code Symbol 11, and apparently on this evidence transferred *T. campestris* to *Dichomitus.* I do not know fruit bodies of *T. campestris* and it may well be that similarities in fruit bodies and especially in the form of skeletal hyphae may warrant the transfer, but the transfer cannot be justified on the basis of cultural similarities, since *Dichomitus squalens* cultures lack the interlocking hyphae that occur in cultures of *T. campestris.*

In my publication on cultural characters as a guide to the taxonomy of the Polyporaceae (Nobles, 1958), I brought together a group of species alike in a number of characters including the presence of microstructures described as nodose-septate hyphae with irregularly thickened walls and fiber hyphae. The species included *Daedalea quercina*, the type of that genus, and *Coriolellus sepium*, the type of *Coriolellus.* After a comparative study of cultures and fruit bodies of six of the species, including the type of *Coriolellus*, Sarkar (1959) presented an emended description of the genus *Coriolellus* giving its cultural characters as well as fruit body characters and listing all six species under the genus *Coriolellus.* In table 2, under Key Code 1.3.8.9., I follow her disposition of the species. Meanwhile, Donk (1966a) transferred the species to *Antrodia*, typified by *A. serpens*, (which I know has similar cultural characters although it is not included in the present study) since *Antrodia* Karst. predated *Coriolellus* Murr. In a paper that came to my attention after table 2 was prepared, Aoshima (1967) has transferred all the species except *Coriolellus sinuosus* to *Daedalea* Pers. ex Fr., a still earlier genus. This pleases me very much, for I have long known that the cultural similarities between the species of *Coriolellus* and the type species of *Daedalea, D. quercina*, suggested close relationship. The recognition of corresponding similarities in fruit bodies and the acceptance of *Daedalea* as the name for the group, with Aoshima's emended description of the genus including Sarkar's cultural characters, indicate the value of correlated cultural and fruit body studies. In his list Aoshima included *D. dickinsii* Yasuda, which I list under Key Code 1.3.8. on the basis of a description published by Bakshi and Bagchee (1950). It is possible that thick-walled, nodose-septate hyphae were missed in their examination of cultures and that they were observed by Aoshima in fruit bodies. Here again a correlated study of fruit bodies and cultures of the species is required. *Trametes* *carbonaria*, transferred to *Daedalea* by Aoshima, also occurs under Key Code 1.3.8. When she was studying the species included by her in *Coriolellus,* Sarkar carefully examined cultures of *T. carbonaria* and deliberately omitted the species from *Coriolellus* because the cultures lacked the thick-walled, nodose-septate hyphae that were present in all species that she assigned to that genus. Here again a correlated study of cultures and fruit bodies is desirable. Cultures of *T. flavescens*, also transferred to *Daedalea* by Aoshima, were described recently by David (1967), and on the basis of her description, which showed the species to have extracellular oxidase and tetrapolar type of interfertility, the species is listed under Key Code 2.3.8. along with the type and a number of other species of *Trametes*. Thus, a consideration of cultural characters may be necessary in deciding the proper disposition of certain species.

Under Key Code 1.3.8.9. (spores cylindric), in addition to the species I have mentioned are *Fomes cajanderi*, *Polyporus durus*, and *Trametes lilacino-gilva*. I am not familiar with fruit bodies of the last two species and can make no comment on their relationships, but I am concerned about the inclusion of *F. cajanderi* in the group. It has obvious similarity with *Fomitopsis rosea*, under Key Code 1.3.8.36. immediately above, but it also has thick-walled, nodose-septate hyphae in culture. Kotlaba and Pouzar (1957) suggested that *Fomes* (*Fomitopsis*) *cajanderi* seemed to occupy a somewhat transitional position between *Fomitopsis* and *Coriolellus*, so it was possible that evidence from fruit bodies also indicated relationship of this species with other species rather than with *Fomitopsis rosea*.

Obviously out of place under Key Code 1.3.8.9. is *Poria xantha*, with the tetrapolar type of interfertility and microstructures that differ from the typical thick-walled, nodose-septate hyphae denoted by Code Symbol 9, but I see no proper niche for it unless it be Special Group I.

The cultural characters of species listed under Key Code 1.3.7. (spores cylindric, brown) and under Key Code 1.3.8. (spores ellipsoid, brown) are similar, especially in the general appearance of cultures and tendency toward formation of strands and plumose mycelium. The two species for which the type of interfertility has been determined are tetrapolar, unlike the majority of species whose cultures lack extracellular oxidase. Three of the species have been assigned to the genus *Serpula*, and *Poria incrassata* has been made the type of the monotypic genus *Meruliporia*. The species may not be closely related to poroid species included in the present study but rather to the Coniophoraceae or some other group.

I would like to refer briefly to the species listed under Key Code 2.3.8. (spores cylindric). Most of the 35 species in the group were originally assigned to *Trametes* and later transferred to genera segregated from that genus. The similarities in cultural characters, including tetrapolarity, suggest close relationship but the even closer similarity among cultures assigned to *Coriolus*, to *Hirschioporus*, to *Pycnoporus*, and *Trametes s. st.* confirm the validity of these genera.

It is not possible to refer to all the groups, but these examples may indicate some practical results of cultural studies in Polyporaceae.

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DISCUSSION

DICK: Do you consider the extracellular oxidase reaction as having arisen once in the Basidiomycetes?

NOBLES: I do not think I want to be quite that definite, although I have said so on a few occasions. It is hard for me to believe that so many species in this group we call Polyporaceae could have so many characters in common without being related. It suggests to me that in this group, at least, there may be one line of development.

DICK: Does anybody know what the distribution of extracellular oxidases would be in the wood-rotting Ascomycetes?

NOBLES: I wish someone would find this out. It is so easy to drop a little guaiacum on cultures and find out what they do.

DICK: Production of these oxidases is easily gained or lost by mutations in particular strains. Wouldn't particular species differ in production as a mutational effect?

NOBLES: I am basing this report only on what I have observed in these cultures of species which are fairly closely related. But in this big group these characters seem to hang together: tetrapolarity, oxidase production, white rots, and preference for hardwoods.

TYLER: It occurs to me that these might be adaptive enzymes which could be induced as a result of a particular substrate on which the fungus is grown, and which might not be there on another substrate.

DICK: This has been shown in some of the polypores. If inducing materials such as xylamine are added to the medium, the enzymes are induced, whereas normally they are not present. The fungus has the capacity to form them provided the requirements are proper. The reactions, then, are reversible.

OLEXIA: Concerning the ideas about brown and white rots—have you been confronted with a white rot fungus which cannot use cellulose, indicating that it may possibly have lost these enzymes?

NOBLES: I am ignorant about the actual practices. I have simply observed that, in general, degradation of cellulose is common to the brown rots. In our experience these fungi always utilize cellulose. Certain species always produce brown rots. Certain other species or strains always cause white rots.

OLEXIA: I have worked to some extent with *Pycnoporus cinnabarinus*, a very attractive organism. I investigated the carbohydrate utilization capacity of the organism and got evidence that it could not degrade cellulose or any other polysaccharide which had a similar linkage, including di- and tri-saccharides. This might indicate that this species might have lost the cellulytic enzymes and merely maintained the lignitic, for I did get the positive reactions of a white rot.

NOBLES: I expect this sort of thing could be found frequently. I know little about these enzyme systems but I do know that some species on the far left side of figure I give a negative reaction for extracellular oxidases. They are actually associated with a white rot so that this reaction isn't really universal by any means, but is only the general pattern.

AMBURGEY: I am working with *Lenzites trabea*, which is a bipolar fungus and which causes a brown rot. Some of the monocaryotic cultures that I have obtained have not had the capacity to decay wood whereas many of the other monocaryotic cultures have. Some of these are still able to break down modified cellulose or cellulose products such as carboxymethyl-cellulose, indicating that there is a complex of enzymes—C-1's, C-X's, and beta-glucosidase—so a mutant obtained in one of these series of enzymes may cause the loss of the capacity to decay wood. I have crossed some of these monocaryons without this capacity and sometimes the dicaryon regains the capacity to cause to decay, but in other cases the dicaryon produced cannot.

PETERSEN: Do you have any data on how many genes may be involved or how many enzyme steps might be involved? How many places can you break it?

AMBURGEY: I have at least one monocaryon that appears to have a mutant C-1 enzyme. This means it can still reduce something like carboxymethyl-cellulose to glucose. In other cases it appears that some isolates are deficient in C-X enzymes. Whether it is one C-X or several C-X's is not quite clear right now.

DONK: I would ask if the use of the many generic names now more-or-less current in Europe means to some degree an endorsement of these genera; is it your intention to accept these genera? I think there is not much difference between *Leptotrimitus* and *Incrustoporia*; the former has effuso-reflexed fruiting bodies but in the latter these are completely resupinate.

NOBLES: I had hoped that this would be noticed because it seems to me it is an indication of relationships. I think they are so closely related as to be one genus. But in some of the others like *Trametes* and its related group and segregates I suspect that they can stand on their own in many cases. I would think certainly that *Incrustoporia* and *Leptotrimitus* might all go together.

BOIDIN: You said that 22 species gave negative results in some oxidase tests, but positive in others. Have you tested for other phenol compounds, such as gallic and tannic acid, which give brown oxidation products which could be confused with excretion? Some phenols (i.e., guaicol) give a very characteristic red color.

NOBLES: I have not followed your system, and I have attempted but not fully employed the method that Dr. Käärik suggested. This is something we should do. We have not tested for the phenol compounds.

BOIDIN: Have you tried more diluted concentrations of phenol which will allow the observation of growth and adaptive formation of enzymes?

NOBLES: I have used 0.5% only.

BOIDIN: I have not looked for possible correlation between presence or absence of oxidase and the cycle's characters. You made a very interesting observation about the Polyporaceae. For 23 species which are without oxidase, 3 are homothallic, 16 bipolar, and only 4 tetrapolar. On the contrary, the tetrapolar species are most numerous in the group with oxidase. This morning, I would have said that the absence of oxidase is an advanced character. However, I believe that you indicated that species without oxidase are primitive, is that not so?

NOBLES: After hearing your paper I wanted to revise mine. Perhaps I have to point the arrow just the other way. It seems to me that tetrapolarity, white-rot production, preference for broad-leaf trees as hosts (and this is true) all go together and would seem to be advanced characters. It is just intuitive, I presume, but it seems to me that they are advanced.

AMBURGEY: To elaborate on what Dr. Boidin has said, returning to *Lenzites trabea*: many of the monocaryons of the species will form fruiting structures (basidiocarps) in culture, which will discharge viable basidiospores and all of the basidiospores have the same mating type as the original monocaryotic culture. These spores will germinate and also will form basidiocarps which produce basidiospores, so there appears to be a homothallic situation without going through the dicaryon. In Dr. Raper's scheme, this would be somewhere between the bipolar and the homothallic, at the top of his chart, and would seem definitely to be a primitive type of fungus because it produces a brown rot, nodose-septate hyphae, and bipolar interfertility.

PETERSEN: I must ask whether you have checked the basidiospores to find out whether they are uninucleate and haploid.

AMBURGEY: I have some evidence that possibly either uninucleate or binucleate basidiospores are produced. I have some evidence that suggests that the monocaryons which fruit in culture contain two nuclei, each of which has the same factor for sexual incompatability. Clamp connections are not formed, but possibly the incompatability genes are at other loci so they may actually be partial heterocaryons.

SMITH: There is a point which concerns the nomenclature for septa of hyphae in the Basidiomycetes. The polypore specialists use the term "nodose-septum" if the cross-wall is accompanied by the specialized clamp connection. They use the term "simple-septate" for a cross-wall unaccompanied by a clamp connection or specialized branch. Since people like Royall Moore have been working, the dolipore septum, which is a truly specialized type of septum, has been described. There is also a septum which does not have a dolipore, and which is not a primary septum. This is a simple curtain-like cross-wall without nuclear or cell division as far as I can tell.

The term "simple septum" would certainly apply very admirably to it. The term "dolipore septum," of course, is self-explanatory. To me the term "nodose-septum" would ordinarily mean that the cross-wall had little granules or nodules. The "simple septum," defined in terms of polypore specialists, seems to be a misnomer. We should not try to define septa in terms of a special branch, but in terms of the characteristics of the septum itself.

DONK: I want to subscribe to Dr. Smith's criticism of the terms "nodose-septate," etc., because in the polypores themselves there are two transverse septa. One is dolipore and the other, in skeletal hyphae for instance, is a pseudo-septum and has no dolipore at all. They are both simple septa.